HUNTING PREY WITH DIFFERENT ESCAPE POTENTIALS— ALTERNATIVE PREDATORY TACTICS IN A DUNE DWELLING SALTICID

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ABSTRACT. Generalist predators hunt a wide range of prey that possess various characteristics affecting the predators' hunting success (e.g., size, ability to detect the threat and defend against it, potential for escape). Therefore, it can be expected that the predator should flexibly react to different prey characteristics, hunting them in prey-specific ways. For a stalking predator a crucial prey feature is its ability to escape. In this study, the alternative prey-catching tactics of a dune-dwelling salticid *Yllenus arenarius* Menge 1868 were analyzed. Four naturally eaten prey taxa, two with a high ability to escape (Homoptera, Orthoptera) and two with a low ability to escape (Thysanoptera, larvae of Lepidoptera), were used. Numerous differences found between the tactics indicate that *Y. arenarius* can not only distinguish between different types of prey, but can also employ specific tactics to catch them. The tactics belong to a conditional strategy and are manifested in alternative: a) direction of approach, b) speed of approach, and c) other prey specific behaviors.

Keywords: Predatory behavior, conditional strategy, spider, Araneae, Salticidae, *Yllenus*

There are numerous examples of alternative phenotypes expressed through animal morphology, life history, and behavior. They are most commonly reported in the field of reproductive biology (reviewed in Gross 1996) and studies of resource-based polymorphisms (reviewed in Skúlason & Smith 1995). The examples are readily interpreted as alternative tactics within a conditional strategy—a concept proposed by Gross (1996). In their theory (Gross & Repka 1998) it is postulated that: a) the tactics involve a choice or decision by the individual; b) the decision is made relative to some aspect of the individual's state or status; c) all individuals in the population have the same genetically-based strategy and the genes for expressing the tactics; d) the average fitnesses of the tactics are unequal; and e) the chosen tactic results in higher fitness for the individual.

The examples of conditional strategies expressed through behavior focus our attention on both the perceptual ability to distinguish between alternative options and the flexibility of animal behavior. Therefore the animals possessing certain limitations to their neural system are of special interest (Jackson 1992; Wilcox & Jackson 1998; Harland & Jackson 2004). Among invertebrates, conditional strategies were found in the behavior of spiders and shown to be common in salticids (Jackson 1992; Edwards & Jackson 1993, 1994; Bear & Hasson 1997).

Conditional strategies are present in both alternative mating tactics and predatory behavior of jumping spiders (Jackson 1992; Edwards & Jackson 1993, 1994; Bear & Hasson 1997). The studies of mating behavior in numerous salticids revealed that the type of male courtship depends on the female's maturity and location (inside vs. outside the nest) (Jackson 1977). Predatory tactics of jumping spiders, conditioned by the prey type and location, provided even more fascinating examples of an extraordinary versatility in these arthropods (Jackson 1992; Jackson & Pollard 1996; Wilcox & Jackson 1998).

Jumping spiders are especially good models to study conditional predatory strategy. This is due to their complex behavior (Richman & Jackson 1992; Jackson & Pollard 1996) and particularly well developed sense of vision (Land 1969a, b; Williams & McIntyre 1980), which enables discernment between various prey characteristics (Harland et al. 1999; Harland & Jackson 2000, 2001, 2002). As a result, the predators can choose a tactic out of an available repertoire on the basis of visual discrimination only.

In many ways, salticid eyes are exceptional among invertebrates. Taken together, the eyes

give a visual field of almost 360° around the cephalothorax (Land 1985). Three pairs of so called "secondary eyes" serve merely as movement detectors, whereas one pair of frontally positioned "principal eyes" has, in fact, much more advanced optical performance than complex insect eyes (Uetz & Stratton 1983; Land 1997; Harland & Jackson 2000) allowing color vision (Blest et al. 1981) and precise shape recognition (reviewed in Forster 1985). The actual distance from which some species can distinguish a prey from a conspecific is equivalent to 47 spider body lengths (Harland et al. 1999). Moreover the spatial acuity of the principal eyes exceeds the spatial acuity of the best seeing insects by tenfold (Harland & Jackson 2004).

The hunting success of a stalking predator is the result of numerous decisions made during the approach stage and capture and depends primarily on the prey's ability to perceive the predator and escape. As summarized by Bear & Hasson (1997), who studied the approaching speed and the striking distance of *Plexippus paykulli* (Audouin 1826), a stalking predator may fail for at least four reasons: if the prey perceives the predator before the attack, releases and escapes after the strike, or spontaneously moves away in the course of its natural activity, even without perceiving the danger. Finally a competitor or the hunter's own predator may influence the outcome of the encounter (before or even after the attack). The analysis of the potential risks reveals numerous trade-offs between contradictory decisions (e.g., slow approach decreases the risk of being noticed but increases the risk of the prey's spontaneous departure). Therefore, each of the alternative behaviors is associated with different pay-offs. To what extent spiders can assess some of the trade-offs and whether they flexibly react in different situations is extremely interesting but poorly represented in the studies (Bear & Hasson 1997). The purpose of the current research is the analysis of prey-specific alternative behaviors in order to assess the extent of the behavioral predatory flexibility of a salticid and to characterize trade-offs that may influence the choice of a tactic.

Yllenus arenarius Menge 1868 is a medium-sized jumping spider with an adult body length of about 7 mm, occurring in Central and Eastern Europe (Logunov & Marusik 2003). This cryptically colored spider dwells in sparse-ly vegetated dunes, where it occupies the areas of bare sand between the grass. An extremely important adaptation for survival in this habitat, which lacks hiding places, is burrowing behavior and the ability to construct sub-sand nests. The nests are built for various purposes (molting, egg-laying, and hibernating) and provide shelter against night-active predators, strong wind and periods of inclement weather (Bartos 2002b). *Yllenus arenarius* is a polyphagous, sit-and-wait predator feeding on a wide range of invertebrates that inhabit open sand or are blown by the wind onto the dune surface from neighboring habitats (Bartos 2004).

METHODS

Prey.—On the basis of a diet analysis carried out before the experiments (Bartos 2004) four taxa of common, natural prey were chosen, markedly different according to their ability to escape. These were: Homoptera, Orthoptera, Thysanoptera, and larvae of Lepidoptera (Table 1). Two of them (Homoptera and Orthoptera) possess wings and/or jumping legs, which enable effective escape and were therefore regarded as prey of high escape risk. Thrips and caterpillars are unable to move quickly and were considered prey of low escape risk.

The prey items were collected in the field by sweep-netting dune grass on the day of the experiment or the day before. They were brought to the lab and kept individually. Each prey item was given to the spider of approximately similar size. In order to reduce mortality of the prey, insects were stored in a refrigerator (5° C) and taken out 15 min before the experiment started.

Predators.—Predators and prey were collected from a dune in Central Poland (Kwilno, 51°59′ N, 19°30′ E). Spiders were collected on the day of the experiment or the day before in order to reduce the influences of rearing conditions on the spider's behavior. Such procedure did not alter the spiders' natural behavior, which may be easily affected by laboratory rearing (Carducci & Jakob 2000; Bartos unpubl. data). This method, however, did not allow us to control for the predator's hunger level. The possible influence of different hunger levels was balanced by random selection of the spider and random choice of one of four prey types. Before the experiments spiders were kept individually in glass containers (height, 10 cm; width, 10 cm) with a layer of dune sand

Table 1.—Prey taxa used in the experiments.

Prey species	Order and family	Ability to escape	Body length (mm)
Psammotettix sp.	Homoptera, Cicadellidae	High	4–5
Omocestus haemorrhoidalis	Orthoptera, Acrididae	High	4–6
Chorthippus brunneus	Orthoptera, Acrididae	High	4–6
Cryptothrips nigripes	Thysanoptera, Phlaeothripidae	Low	2
Thrips trehernei	Thysanoptera, Thripidae	Low	1
Chirothrips manicatus	Thysanoptera, Thripidae	Low	1
Pyralis farinalis	Lepidoptera, Pyralidae (larvae)	Low	4–8
Autographa gamma	Lepidoptera, Noctuidae (larvae)	Low	4–8

on the bottom. Adult individuals of *Y. arenarius* are characterized by strong sexual dimorphism expressed in color and pattern. The intersexual differences appear after the final molt and may influence the hunting behavior of one sex (Givens 1978; Bartos unpubl. data), therefore only juveniles (body length ca. 4.5 mm) and females (body length ca. 6 mm) were used in the experiments. Approximately the same number of individuals from each age group was used. Each spider was chosen randomly and used only once in the whole set of tests. The total number of spiders tested was 981, but only in ca. 25% were hunting sequences observed. The experiments in which no hunting behavior was present (e.g., because the spider ignored the prey or the prey escaped before it was approached) were not included in the analysis. The number of experiments in which the spider hunted the prey is given as *n*.

Experimental procedure.—Experiments were carried out within a white cardboard arena (height, 15 cm; diameter, 20 cm) with a 1 cm-thick sand layer on the bottom. All the experiments were conducted between 09:00 and 16:00 hours (laboratory light regime, 12L:12D, lights coming on at 08:00 hours). Lighting was from a 100W PILA incandescent lamp bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena. Spiders were placed within the arena and, after 1 min, a prey item was introduced about 8 cm from the spider. The prey was dropped approximately 30° to the left or right from the main eye's optical axis to allow the experimenter to record the moment when the predator perceived the prey. The prey was left with the spider for 15 min. The hunting behavior was recorded with a camera placed above the arena.

Data analysis.—Movies with hunting sequences were analyzed, the behaviors observed, and the hunting success was recorded. The complete sequences of hunting, namely those that started with the first dynamic behavior (run), and that ended with subduing the prey were used to draw flow diagrams (Figs. 1–4). If there were multiple attacks of a spider on the same prey, only the first hunting sequence was included. The percentage of individuals that expressed certain behaviors is indicated by the width of the line that leads to the behavior and by the number above the line. The numbers in some paths do not add up to 100% due to rounding.

Since the modes of hunting prey with both high and low ability to escape demonstrate many similarities, the complete series of behavioral units typical for hunting each kind of prey is given only in the first description below. In the account of the hunting sequence for prey that cannot escape, only a description of the prey-specific behaviors is presented. Names of other already reported components of salticid behavior are taken from a classic paper by Forster (1977).

All statistical procedures followed those described by Zar (1984). To test the differences in frequency of behavior in hunting different prey types, the Pearson's chi-squared test was used.

RESULTS

The pattern of hunting prey with different escape potentials.—When hunting prey with a high ability to escape, irrespective of the prey taxon, the first easily discernible element was "alert" characterized by movement of the cephalothorax or of the whole body, which resulted in directing the main eyes towards the prey (Figs. 1–4). Spiders observed the prey for
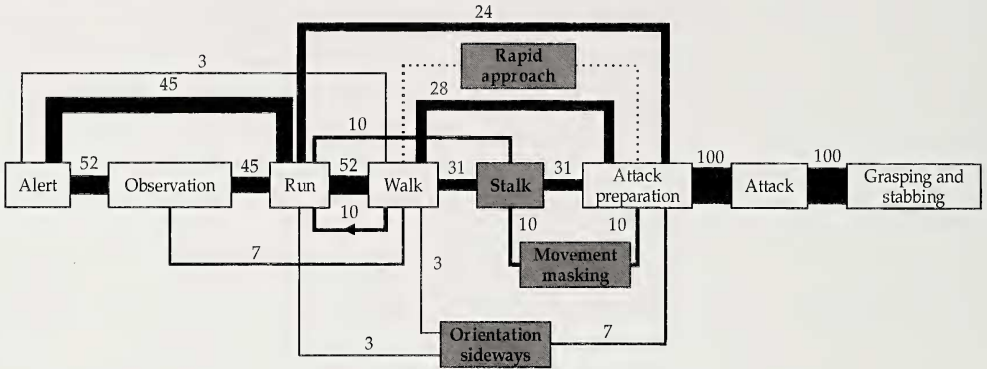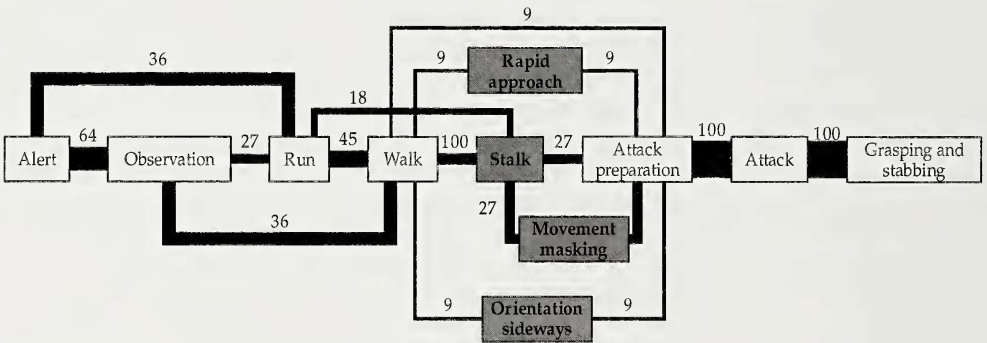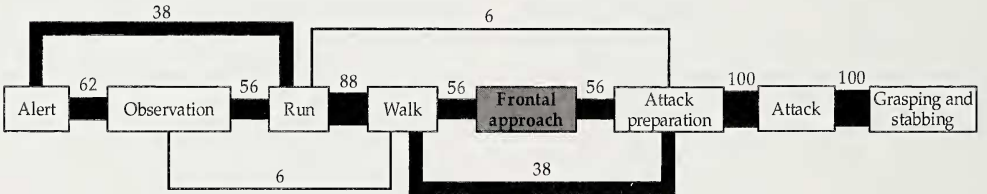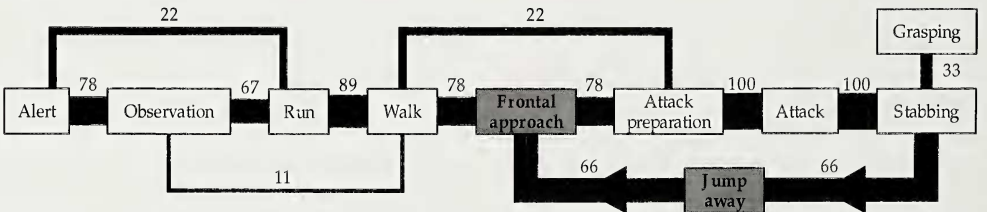
Figures 1–4.—Flow diagrams of *Y. arenarius* hunting four prey taxa. 1. Homoptera (*n* = 29); 2. Orthoptera (*n* = 11); 3. Thysanoptera (*n* = 16); 4. larvae of Lepidoptera (*n* = 9). Transition frequencies are indicated by the per cent numbers and by an appropriate line width. Dotted line symbolizes the behavior that was not observed in the complete hunting sequence but was commonly recorded in incomplete sequences. Grey boxes indicate prey-specific behaviors. The sequence should be read from left to right unless indicated by an arrow.

usually less than a minute and ran towards it in bursts. The closer spiders got to the target, the slower was their movement. They decelerated to a walk and subsequently stalked prey with a slow, "cat-like" motion. Another slow type of approach called "movement masking" was observed when the prey moved and froze alternately and, following the prey movements, the spider approached only when the prey changed its position; e.g., began cleaning its body or slowly moving. The spider froze or decelerated when the prey stopped moving. An alternative mode of approach using a long jump or quick run in the direction of prey was called "rapid approach" (Figs. 1, 2). Spiders using this tactic landed or stopped running very close to the target and attacked after only a short sequence of preparation for the attack. In a few cases the predators did not approach directly, but orientated sideways going round the prey with a rapid, crab-like movement (Figs. 1, 2). During the activity, spiders always orientated themselves towards the prey, but never approached frontally.

Directly before the attack, a series of four characteristic preparatory movements was observed. Spiders a) lowered their bodies spreading legs sideways, b) attached dragline to the sand surface, c) rapidly pushed sand with the fourth pair of legs, and finally d) raised the first and sometimes also the second pairs of legs in the direction of the prey. The attack occurred in all cases of hunting Homoptera and Orthoptera by means of a jump and took place soon after the frontal leg raising. After landing on the prey's back, the insect was embraced with legs and finally pierced with fangs. In a few cases, prey managed to escape or was released after the first direct contact and the predator usually withdrew. However, the prey was neither observed by the spider after such abandonment nor was the attack repeated.

The sequence of events in hunting thrips and caterpillars was shorter and less complex, but most units described in hunting Homoptera and Orthoptera were also present here (Figs. 3, 4). The specific behaviors concerned the direction of approach or prey handling after attack. Spiders approached the anterior part of the prey's body rather than the abdomen. Such behavior, defined as "frontal approach," was characterized by circling the prey (if the prey was not facing the spider before approach). As a consequence of this tactic the spider found

itself in front of the moving prey, either waiting on its supposed track or actively approaching the prey. After the attack preparation, spiders jumped on the prey or walked and stabbed it with most bite punctures found on the dorsal side of the second and the third segments of the thorax. Caterpillars were most frequently released after venom injection and, after jumping away from the caterpillar, the predator stayed close, constantly observing the wriggling prey. After a period of time, the attacks were repeated and up to eight strikes were observed before the prey was finally subdued.

Behavioral prey-specificity.—Prey-specific behaviors were observed when the predator was in the proximity of the target. While moving towards Homoptera and Orthoptera, the predator decelerated and, when close, stalked them. Such behavior was almost never observed in approaching thrips and caterpillars (Fig. 5) ($\chi^2 = 46.32$, $df = 3$, $P < 0.001$). Another behavior specific for hunting more mobile prey was "movement masking," which was never observed in approaching caterpillars (Fig. 6) ($\chi^2 = 49.41$, $df = 2$, $P < 0.001$). "Movement masking" could not be recorded when hunting thrips since it requires the prey to alternately slow down and then speed up. This does not occur in thysanopteran movement, which is generally uniform in speed and with only sporadic pauses when on the open sand. Two other behaviors specific for hunting Homoptera and Orthoptera were "rapid approach" ($\chi^2 = 10.81$, $df = 3$, $P < 0.05$) and "orientation sideways" ($\chi^2 = 9.32$, $df = 3$, $P < 0.05$). Neither of the behaviors was observed in cases of hunting Thysanoptera and larvae of Lepidoptera (Figs. 7, 8).

Interestingly, the prey of high and low escape risk was attacked from different directions. While thrips and caterpillars were circled and approached from their front side, no such definite attack direction was preferred in hunting Homoptera and Orthoptera ($\chi^2 = 97.74$, $df = 3$, $P < 0.001$) (Fig. 9). The mode of handling prey directly after attack also differed between the groups ($\chi^2 = 75.32$, $df = 3$, $P < 0.001$). Homoptera and Orthoptera were never released after venom injection (Fig. 10). In only one out of 34 episodes of hunting thrips was the prey released and, after a short time, attacked again and subdued. Repeated attacks with venom injection were followed by release of the prey. Hunting prey of low and high
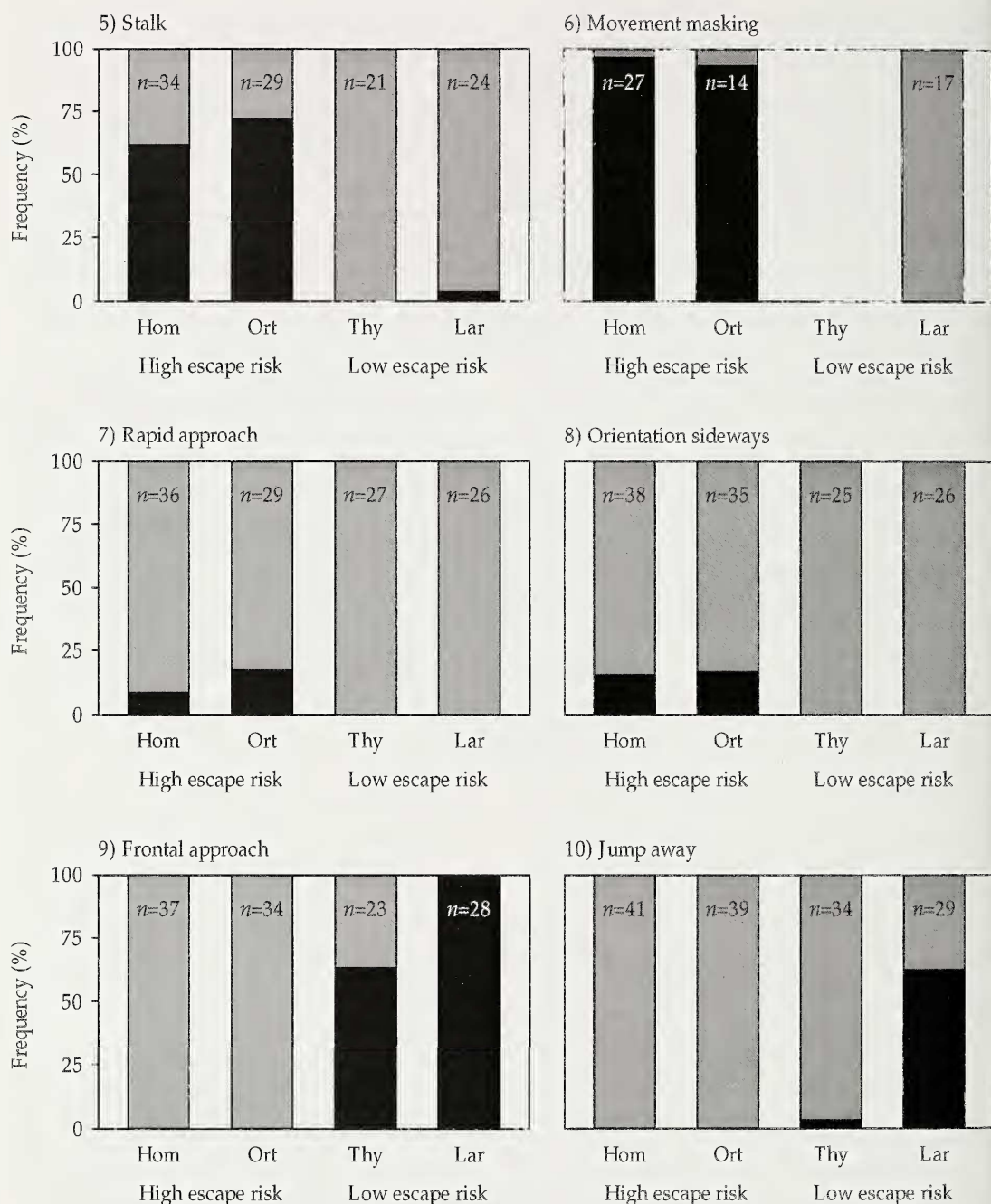
Figures 5–10.—Frequency of six prey-specific behaviors in hunting Homoptera (Hom), Orthoptera (Ort), Thysanoptera (Thy) and larvae of Lepidoptera (Lar) by *Y. arenarius*. The behaviors are: 5. Stalk; 6. Movement masking; 7. Rapid approach; 8. Orientation sideways; 9. Frontal approach; and 10. Jump away.

escape risk differed also according to the hunting success ($\chi^2 = 7.56$, $df = 1$, $P < 0.01$). All cases of catching thrips ($n = 34$) and caterpillars ($n = 29$) were successful in comparison to 95% of homopterans ($n = 41$) and 82% of orthopterans ($n = 39$).

DISCUSSION

The pattern of hunting prey with different escape potentials.—The hunting behavior observed in *Y. arenarius* was similar to those of other non-specialized salticids approaching comparable prey (Forster 1977, 1982; Edwards

& Jackson 1993, 1994; Bear & Hasson 1997). Three phases: orientation, pursuit, and capture, reported by Forster (1977) were easily discernible in hunting all four prey taxa. Although the general pattern of approach was similar for hunting prey of both high and low ability to escape, the differences in hunting them were clearly discernible only when the predator got nearer to its prey, namely at the stage of pursuit and capture (Figs. 1–4). Obviously, once the predator was closer to the prey, the prey could more easily perceive the predator and escape, if able to do so. At the beginning of the hunting session, both prey types were approached in a similar way from a relatively long distance away: quickly and without any apparent measures taken to reduce the predator's visibility to the prey (Figs. 1–4). Such distance-dependent behavior is typical for many predators that stalk their prey (Curio 1976).

Alternative tactics.—Numerous differences found between the tactics of hunting four prey taxa indicate that *Y. arenarius* can both distinguish between different types of prey and employ a specific mode of hunting to catch them. The choice of a tactic takes place after a period of observation. According to the definition of the conditional strategy summarized in the introduction (Gross & Repka 1998), the tactics observed in *Y. arenarius* may be defined as a part of conditional strategy in which the decisions concerning the mode of approach seem to depend primarily on both the prey's ability to escape and the predator's visibility to the prey. The behavior that increases hunting success must obviously result in higher fitness to the predator. The alternative tactics were expressed in four aspects of hunting: direction and speed of approach, specific behaviors and finally jumping distance, which was discussed elsewhere (Bartos 2002a).

Direction of approach: Both prey of low and high risk of escape were approached differently. No specific path was preferred when hunting Homoptera and Orthoptera. They were approached directly irrespective of their position. Such a path might increase hunting success not only because it is the fastest way of reaching the target, but also because it reduces the risk of being perceived by the prey if it was circled. These advantages of direct approach are reflected in the widespread occurrence of the tactic among salticids (Freed 1984; Edwards & Jackson 1993, 1994; Bear & Hasson 1997).

"Frontal approach," the direction specific for prey that had limited ability to escape, was recognizable shortly after the spider had moved in the direction of the prey. This suggests both quick prey recognition and flexible choice of hunting tactic. Running around prey that cannot escape may be advantageous for several reasons. First, the predator attacking frontally grasps the prey by the dorsal side of the thorax and head, thus neutralizing the prey's jaws, and defensive fluids commonly spit out of the prey's mouth (Edwards & Jackson 1993; Salazar & Whitman 2001; Bartos unpubl.). A wriggling caterpillar is also less effective at throwing the spider away and hitting it against the ground if the spider does not jump away. Furthermore, the attack from the front side enables firm prey grasping (proportional from both sides) and fang piercing which, in consequence, allows precise venom injection. Logically, the faster the prey is paralyzed, the lower risk of injury or perception of the prey (and the spider) by other predators.

It is interesting that prior to the strike on caterpillars and thrips the spiders kept a close and fairly constant distance to the prey's head, but avoided premature contact with the prey's body, withdrawing when the prey approached too close. Such behavior was also reported by Edwards & Jackson (1993), which suggests that early detection may also play a role in the case of prey with low ability to escape, possibly diminishing the predator's chances to strike and grasp the prey precisely.

Speed of approach: Although in my research the predator's velocity was not directly measured, it is quite clear, analyzing certain behaviors preceding the attack, that prey with high risk of escape is approached slowly ("stalk" and "movement masking") while prey with low risk of escape is approached without such preventative measures. This kind of a relationship between the speed of approach and distance to prey has been neatly shown by Bear & Hasson (1997) in their study of *P. paykulli*.

Prey-specific behaviors: Some prey-specific behaviors observed in the course of prey capture in *Y. arenarius* (e.g., "stalk," "orientation sideways," "frontal approach") are also reported in the studies of other salticids (Forster 1977, 1982; Edwards & Jackson 1993, 1994) and seem to be universal elements of the hunting strategy in jumping spiders. However, during the research some prey-

specific behaviors (e.g., "movement masking," "rapid approach," "sand firming before the jump," "jump away") were not reported elsewhere and therefore they are possibly unique for *Y. arenarius*. Some of the behaviors constitute essential components of the alternative tactics and therefore are discussed in detail.

"Movement masking" seems to be a very effective tactic against more mobile prey. It is in many aspects similar to "opportunistic smokescreen behavior" reported for *Portia* approaching prey on alien webs (Wilcox et al. 1996; Jackson et al. 2002) and even more to "cryptic stalk" observed only when *Portia* approaches other salticids (Harland & Jackson 2001). In all cases the predators exploit situations in which the prey's ability to detect the spider is impaired. Web-invaders approach host spiders using a smoke-screen when the host webs are subjected to vibrations masking the predator's footsteps. While approaching egg sacs or insects ensnared in the web, salticid web-invaders do not perform the smoke-screen behavior (Wilcox et al. 1996; Cerveira et al. 2003). *Portia* stalking prey cryptically holds its palps back beside the chelicerae and uses a slow, choppy gait, freezing when faced by its salticid prey. Harland & Jackson (2001) observed that most salticids fail to recognize a cryptically stalking *Portia* as predator. Similarly *Y. arenarius* approaches cryptically when the prey moves (changing position, cleaning legs or antennae), which decreases its ability to perceive a moving predator. Such behavior is observed, however, only when the prey is able to escape. Therefore, although "opportunistic smokescreen behavior" and "cryptic stalk" have been only recorded for web-invading araneophagic spartaeines (Wilcox et al. 1996; Cerveira et al. 2003), in a broad sense the general pattern of behavior may be widespread among other salticids.

Some spiders that hunted the prey with high ability to escape did not stalk but approached their prey rapidly. This alternative way of approach, which obviously increases the risk of a prey's escape, may also have some advantages. Although the conditions influencing the choice of the tactic cannot be precisely determined at this stage of analysis, one of the possible factors that may play a role seems to be the risk of the prey's spontaneous departure (Bear & Hasson 1997). Both Homoptera and Orthoptera unpredictably move from one place to another, therefore the high risk of being noticed by the prey may be balanced by the advantage of quick and sudden attack.

"Orientation sideways" was another intriguing behavior observed in close proximity to the prey. Similarly to rapid approach, orientation sideways also deviated from the general pattern of approach to the prey with high ability to escape, which may be summarized as: "the closer to the prey, the less conspicuous the predator's behavior." Such pattern may also be observed in the gradual changes of approaching speed in *P. paykulli* (Bear & Hasson 1997) and results from the increasing ability of the prey to detect the predator as it comes nearer. The possible function of the behavior seems to primarily be identification. Sideways movements enable prey perception from different angles and as a result give a three-dimensional representation of the observed object. Such behavior may also improve estimation of distance to the prey.

Orientation sideways must significantly increase the risk of being detected, but there are, however, circumstances that may counterbalance the risky tactic. The most likely factors seem to be those connected with potential threat that a prey animal may pose to the predator. As a polyphagous predator *Y. arenarius* also hunts prey possessing powerful jaws and stings (Bartos 2004). Some of the prey animals (e.g., solitary bees, ants) resemble those which were frequently observed to parasitize or feed on the spider (e.g., pompilid wasps, other ant species or castes) (Bartos unpubl.). Therefore, precise prey identification and determination of the area of grasping and venom injection are extremely important tasks.

"Jump away," the behavior specific for *Y. arenarius* hunting caterpillars, has not been described in other studies on salticids hunting insect larvae (Edwards & Jackson 1993, 1994; Bear & Hasson 1997), but similar behavior was reported for several species of *Aelurillus* hunting wingless ants (Li et al. 1999). "Jump away" seems to be a good adaptation to minimize the risk of interference with the spider's own predators (Bear & Hasson 1997) and reduce the possibility of getting injured by the prey. On the surface of bare sand dunes, any movement may attract predators. The most serious threat constitutes tiger beetles, robber-flies, and ants, or some less numerous vertebrates such as birds or lizards (Bartos unpubl.). The best strategy to

avoid the movement-sensitive predators would be to stay motionless and keep away from any object that attracts a predator's attention (Pearson 1988). A cryptically colored spider that stealthily waits until the prey is paralyzed obviously reduces both the risk of being detected by its own predators and the risk of getting injured by the prey than the one that tries to overpower a writhing caterpillar.

The prey with high risk of escape was never released after being captured. This is presumably because the period from venom injection to prey immobilization would be long enough to enable efficient escape or blowing the prey away by wind. My numerous observations of orthopterans and homopterans jumping for several minutes with a spider on their backs before they became paralyzed, support this assumption. Similarly, thrips, which are fairly delicate but winged prey with markedly limited escape potential, were not released after attack. They were, however, usually kept hidden between the legs and under the predator's body, therefore their visibility and the risk of injury to the spider was possibly limited.

ACKNOWLEDGMENTS

LITERATURE CITED

Bartos, M. 2002a. Distance of approach to prey is adjusted to the prey's ability to escape in *Yllenus arenarius* (Araneae, Salticidae). Pp. 33–38. *In* European Arachnology 2000: Proceedings of the 19th European Colloquium of Arachnology, Aarhus. (S. Toft & N. Scharff, eds.). Aarhus University Press, Aarhus, Denmark.

Bartos, M. 2002b. The sub-sand nests of *Yllenus arenarius* (Araneae, Salticidae): structure, function and construction behavior. Journal of Arachnology 30:275–280.

Bartos, M. 2004. The prey of *Yllenus arenarius* (Araneae, Salticidae). Bulletin of the British Arachnological Society 13:83–85.

Bear, A. & O. Hasson. 1997. The predatory response of a stalking spider, *Plexippus paykulli*, to

camouflage and prey type. Animal Behaviour 54:993–998.

Blest, A.D., R.C. Hardie, P. McIntyre & D.S. Williams. 1981. The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider. Journal of Comparative Physiology 145:227–239.

Carducci, J.P. & E.M. Jakob. 2000. Rearing environment affects behaviour of jumping spiders. Animal Behaviour 59:39–46.

Cerveira, A.M., R.R. Jackson & E.F. Guseinov. 2003. Stalking decisions of web-invading araneophagic jumping spiders from Australia, Azerbaijan, Israel, Kenya, Portugal and Sri Lanka: the opportunistic smokescreen tactics of *Brettus, Cocalus, Cyrba* and *Portia*. New Zealand Journal of Zoology 30:21–30.

Curio, E. 1976. The Ethology of Predation. Series in Zoophysiology and Ecology, Volume 7. Springer-Verlag, Berlin. 250 pp.

Edwards, G.B. & R.R. Jackson. 1993. Use of prey-specific predatory behaviour by North American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. Journal of Zoology (London) 229:709–716.

Edwards, G.B. & R.R. Jackson. 1994. The role of experience in the development of predatory behaviour in *Phidippus regius*, a jumping spider (Araneae, Salticidae) from Florida. New Zealand Journal of Zoology 21:269–277.

Forster, L.M. 1977. A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). New Zealand Journal of Zoology 4:51–62.

Forster, L.M. 1982. Vision and prey-catching strategies in jumping spiders. American Scientist 70:165–175.

Forster, L.M. 1985. Target discrimination in jumping spiders (Araneae: Salticidae). Pp. 249–274. *In* Neurobiology of Arachnids. (F.G. Barth, ed.). Springer-Verlag, Berlin.

Freed, A.N. 1984. Foraging behaviour in the jumping spider *Phidippus audax:* bases for selectivity. Journal of Zoology (London) 203:49–61.

Givens, R.P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). Ecology 59:309–321.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology & Evolution 11:92–98.

Gross, M.R. & J. Repka. 1998. Stability with inheritance in the conditional strategy. Journal of Theoretical Biology 192:445–453.

Harland, D.P. & R.R. Jackson. 2000. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. Journal of Experimental Biology 203:3485–3494.

Harland, D.P. & R.R. Jackson. 2001. Prey classification by *Portia fimbriata*, a salticid spider that

specializes at preying on other salticids: species that elicit cryptic stalking. Journal of Zoology (London) 255:445–460.

Harland, D.P. & R.R. Jackson. 2002. Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. Journal of Experimental Biology 205: 1861–1868.

Harland, D.P. & R.R. Jackson. 2004. Portia perceptions the umwelt of an araneophagic jumping spider. Pp. 4–40. *In* Complex Worlds from Simpler Nervous Systems. (F.R. Prete, ed.). MIT Press, Cambridge, Massachusetts.

Harland, D.P., R.R. Jackson & A.M. Macnab. 1999. Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals. Journal of Zoology (London) 247: 357–364.

Jackson, R.R. 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). Animal Behaviour 25:953–957.

Jackson, R.R. 1992. Conditional strategies and interpopulation variation in the behaviour of jumping spiders. New Zealand Journal of Zoology 9:99–111.

Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. Annual Review of Entomology 41:287–308.

Jackson, R.R., S.D. Pollard & A.M. Cerveira. 2002. Opportunistic use of cognitive smokescreens by araneophagic jumping spiders. Animal Cognition 5:147–157.

Land, M.F. 1969a. Structure of the retinae of the eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology 51:443–470.

Land, M.F. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology 51:471–493.

Land, M.F. 1985. Fields of view of the eyes of primitive jumping spiders. Journal of Experimental Biology 119:381–384.

Land, M.F. 1997. Visual acuity in insects. Annual Review of Entomology 42:147–177.

Li, D., R.R. Jackson & D.P. Harland. 1999. Prey-capture techniques and prey preferences of *Aelurillus aeruginosus, A. cognatus,* and *A. kochi,* ant-eating jumping spiders (Araneae: Salticidae) from Israel. Israel Journal Zoology 45:341–359.

Logunov, D.V. & Y.M. Marusik. 2003. A Revision of the Genus *Yllenus* Simon, 1868 (Arachnida, Araneae, Salticidae). KMK Scientific Press Ltd., Moscow. 167 pp.

Pearson, D.L. 1988. Biology of tiger beetles. Annual Review of Entomology 33:123–47.

Richman, D.B. & R.R. Jackson. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). Bulletin of the British Arachnological Society 9:33–37.

Salazar, B.A. & D.W. Whitman. 2001. Defensive tactics of caterpillars against predators and parasitoids. Pp. 161–207. *In* Insects and Plant Defense Dynamics. (T.N. Ananthakrishnan, ed.). Science Publishers, Plymouth, UK.

Skúlason, S. & T.B. Smith. 1995. Resource polymorphisms in vertebrates. Trends in Ecology & Evolution 10:366–370.

Uetz, G.W. & G.E. Stratton. 1983. Communication in spiders. Endeavour, N. S. 7:13–18.

Wilcox, R.S. & R.R. Jackson. 1998. Cognitive abilities of araneophagic jumping spiders. Pp. 411–433. *In* Animal Cognition in Nature: the Convergence of Psychology and Biology in Laboratory and Field. (R.P. Balda, I.M. Pepperberg & A.C. Kamil, eds.). Academic Press, New York.

Wilcox, R.S. & R.R. Jackson. 2002. Jumping spider tricksters: deceit, predation, and cognition. Pp. 27–33. *In* The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition. (M. Bekoff, C. Allen & G.M. Burhgard, eds.). MIT Press, Cambridge, Massachusetts.

Wilcox, R.S., R.R. Jackson & K. Gentile. 1996. Spider web smokescreens: spider tricksters use background noise to mask stalking movements. Animal Behaviour 51:313–326.

Williams, D.S. & P. McIntyre. 1980. The principal eyes of a jumping spider have a telephoto component. Nature 288:578–580.

Zar, J.H. 1984. Biostatistical Analysis. 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.